

PLATE 13.

- Fig. 4. *Columbula picus*, left wing; carpal covert and remex; series of coverts and secondaries: showing the eutaxic condition.
- Fig. 5. *Geotrygon montana*, left wing; 1st primary; carpal remex and covert; series of secondaries and coverts: showing reduced diastataxic condition.
- Fig. 6. *Starnanias cyanocephala*, left wing; carpal remex and covert; six secondaries and coverts in even series. Eutaxic arrangement.
- Fig. 7. *Turtur chinensis*, left wing; carpal covert and remex; four secondaries and coverts; diastataxic gap with covert; two secondaries with coverts.

Some Facts concerning the so-called "Aquintocubitalism" in
the Bird's Wing. By W. P. PYCRAFT, A.L.S.*

[Read 16th March, 1899.]

(PLATES 14-16.)

CONTENTS.

	Page
Introductory Remarks	236
Eutaxic and Diastataxic Wings	237
The Embryo Wing	238
Summary of the foregoing Remarks	241
Evidence in support of the above Conclusions	241
A possible Objection.....	244
The Carpal Covert and Remex	245
Explanations of Diastataxy	246
Exceptions	247
Facts correlated with Diastataxy	249
Some Degenerate Wings	250
The Probable Origin of the Diastataxic Wing	252
Diastataxy as a Factor in Classification.....	254

Introductory Remarks.

THE feathers in the typical bird's wing, *e. g.*, the Common Fowl, are divisible into two groups—tectrices or coverts, and remiges or flight-feathers, commonly known as "quills."

The remiges form a single row of feathers running along the post-axial border of the wing from the tip of the index-digit inwards to the elbow-joint. Those of the hand constitute the primaries, those of the forearm the secondaries. With the primaries we have little or nothing to do in this connection; suffice it to say that they never, in the Carinatae, exceed 12 in

* Cf. Editorial footnote on p. 21

number. The number of the secondaries varies greatly from 9 to 37. Though the primaries are packed closely together at their bases, the secondaries are more or less widely spaced (Pl. 14. fig. 5). The exigencies of flight demand this.

The tectrices are separable into several distinct series, forming the major, median, minor, and marginal coverts, to which may be added the *ala spuria*, the *hypopteron*, and *parapteron*. With these last we have nothing to do now. The tectrices clothe the dorsal and ventral surfaces of the wing. The major coverts are the most post-axial, and are seated in pairs on the bases of the remiges—two to each remex, one dorsal and one ventral—to which they are firmly attached. The median form the row next in front of the major coverts, both on the dorsal and ventral surface. There is never more than one row on the dorsal or ventral surface. The minor lie beyond the median coverts, and vary from 1 to 4-5 rows on both aspects of the wing. Beyond these are the marginal coverts; they occupy the pre-axial border of the wing, and help to clothe both the dorsal and ventral surfaces.

A reference to Pl. 14. fig. 5 will make this much more clear than mere description. Questions concerning the overlap, variations in the number of rows of minor and marginal coverts, their length, the absence of more or fewer of these rows on the arm or manus in different groups, need not be discussed here. One point, however, is noteworthy. Sundevall (7), and later, and more correctly, Wray (8) pointed out that the major and median coverts of the ventral aspect of the wing turn their ventral surfaces downwards as do the remiges, and not *upwards* as do all the other coverts of the under surface. Wray's interpretation of this was, that these feathers had been slowly carried round from the dorsal surface of the wing, whilst the tectrices of the under surface were separately derived from the ventral surface of the body.

Eutaxic and Diastataxic Wings.

The Bird's wing may assume one of two forms, known hitherto as (1) the Quintocubital, and (2) the Aquintocubital (p. 238). The two may readily be distinguished. In the former, each pair of secondary major coverts embraces a remex between them; in the latter, the remex from between the 5th pair of coverts is apparently missing—hence the name "aquintocubital." The perfectly regular arrangement of the coverts in such a wing, and the presence of a more or less distinct gap between the 4th

remex and that next succeeding it, seemed to justify the conclusion that a remex had been lost—that the wing had undergone a reduction of the original number of its remiges by the loss of the 5th quill. The aim of the present paper is to show that no such loss has taken place. The 5th remex has lost its original relations, but *not* its existence.

Before proceeding further, it will be well to say a few words concerning the terms which have been proposed as substitutes for the older and less exact “Quinto-” and “Aquinto-cubital.” At the time this paper was read the names Stichoptylic for the former, and Apoptylic for the latter were used. These were suggested to me by Prof. E. Ray Lankester, and were certainly preferable to those which we both desired to supplant. But it will be remembered that Mr. P. Chalmers Mitchell, in the course of his paper dealing with this same question, suggested the names Eutaxic for the quintocubital or stichoptilic form, and Diastataxic for the aquintocubital or apoptilic. His names not only have priority over mine, or, rather, Prof. Lankester’s (his paper having been read before mine), but they are, I think, actually preferable; hence, throughout this paper, I shall adopt the terminology proposed by him. Moreover, by doing this I shall be rendering a service to my readers, by saving them the labour of keeping in mind the values of some half-dozen names for what may be called the positive and negative of one and the same thing.

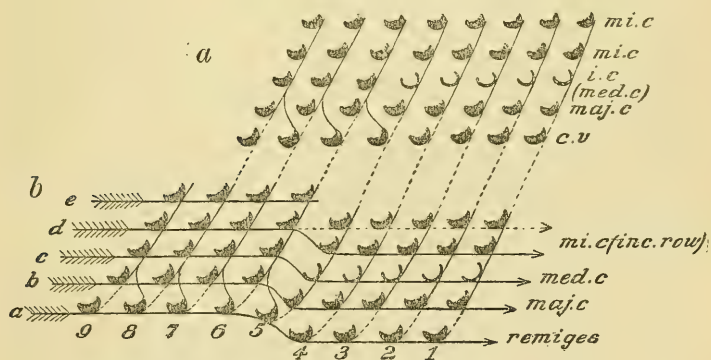
The Embryo Wing.

In all wings, the feather rudiments appear first along the post-axial border of the wing; those representing the remiges and their major coverts appearing simultaneously, and sometimes together with very faint traces of one or more of the pre-axial rows representing the median and minor coverts. At this stage, it is often not possible to say whether a wing will ultimately prove eu- or diasta-taxic. The change takes place, however, generally at the close of this phase of development. As the rudiments of the median and minor coverts become more distinct, it will be noticed that the papillæ representing the remiges 1-4 no longer form an unbroken series with those running from this point inwards, but that they have moved backwards and downwards; sometimes this is very marked, sometimes only very slightly so. The hitherto unbroken series

now becomes more or less distinctly divided into two portions, thus:—; at the same time, it is noticeable that this shifting of the outer remiges backwards may also be accompanied by an outward movement towards the tip of the wing. Sometimes all four remiges participate in this outer movement, sometimes only the 1st or 1st and 2nd become notably disturbed.

The movement of the remiges is in all cases accompanied by a corresponding movement on the part of the coverts associated therewith, from the post- to the pre-axial border. The result, when the wing is viewed as a whole, seems to show that a process of "faulting" has taken place, the major, median, and one or more rows of minor coverts from 1 to 5 in each row having slipped backwards so as to break the connection with their several rows proximad of this point; each row—or, more correctly, the first 3 or 4 rows—now runs, not in a continuous line with that of its series, but between this and that immediately behind it (fig. 1, *b*). The disturbed rows, however, seem to readjust

Fig. 1.



Shifting of wing-coverts and remiges. *a*, before; *b*, after.

themselves very quickly so as once more to form continuous lines with the more proximal feathers; as, in the typical diastataxic wing, it will be found that, not counting the remiges, uniformity is regained at the 4th row, or rather a semblance of uniformity, inasmuch as this row is really made up of two rows. This is shown in the diagram (fig. 1, *b*). Here the 3rd row of these downwardly shifted coverts appears as an intercalary row, the 4th row becoming continuous with that of the

5th, thus affording at the same time evidence in favour of the view adopted in this paper, that all these coverts have shifted backwards. Pl. 15. fig. 1 represents the wing of an embryo Pigeon showing this intercalary 3rd row very clearly.

Only one row of ventral coverts appears to participate in the general disturbance which we have traced on the dorsal surface in connection with this backward and downward motion of coverts 1-5 and remiges 1-4. This is well seen in fig. 3, Pl. 14, representing a ventral view of the wing of an embryo *Machetes pugnax*.

Before passing on to consider what is, apparently, the only possible objection to the explanation of the phenomena here set forth, I would draw attention to the accompanying diagrams.

Fig. 1 *a* (p. 239) represents the arrangement of the cubital coverts and remiges in the eutaxic wing as far inwards as the 9th remex. Fig. 1 *b* shows the effect of a backward and outward shifting of remiges 1-4 and coverts 1-5 from the major coverts forwards; *i. e.*, a portion of each horizontal row of coverts from 1-5 from the major coverts forwards to the tectrices minores, thus converting the eu- into the diasta-taxic wing. The bending of the horizontal lines serves to indicate the amount of shifting which the remiges and coverts have undergone. The arrow "*d*" has been made to "dip" like the arrows *a*, *b*, *c*, so as to indicate the amount of shifting of each row; it has also, by means of a dotted line, been made to pass straight outwards to indicate the restoration of parallel series. But it must be remembered that these restored rows are composed of feathers belonging to two different rows. Thus coverts 1-5 of the 2nd row of minor coverts now become serial with the coverts of the 1st row from the 6th inwards, the coverts 1-5 of the 1st row having been cut off to form a series by themselves—the intercalary row. This intercalary row actually obtains in a more or less well-developed form in all diastataxic wings, and this diagram enables us to see how it may have come into existence. In so far as the diagram is concerned, it is perfectly true that the 1-5 coverts of the median row could equally well be regarded as an intercalary row. The size and position of these feathers in the adult probably account for their retention in the series to which they belong. The row (1-5) immediately in front are smaller and more easily isolated; hence these in the adult become the intercalary row.

The diagram just described (fig. 1, *a*, *b*), to show how the eu- may have been transformed into the diasta-taxic wing, can be

readily constructed by the reader by laying over fig. 1 *a* a piece of transparent paper and marking over remiges 1-4 and coverts from 1-5 in each row. This being done, shift the paper backwards and slightly forwards so that the major coverts 1-5 come to lie parallel with the interspace between the remiges and major coverts proximal to 5, as has been done in fig. 1 *b*. This gives the two broken rows of coverts (major and median) and the intercalary row (3), which exactly agrees with actual wings (*e. g.*, Pl. 15. fig. 1).

Inasmuch as by this artificial mechanical shifting and re-arrangement of the feathers of the anterior end of the dorsal aspect of the forearm, all the features of the diastataxic wing can be demonstrated, it may be reasonably contended that a strong degree of probability has been brought forward in support of the view that the phenomena of diastataxy are due to a backward and downward shifting of the remiges and their coverts.

Summary of the foregoing Remarks.

To summarize briefly, the contention of the present paper is:—

(1) That there is no evidence in support of the hypothesis that diastataxy is due to the absence of a remex.

(2) There is a very considerable amount of evidence to show that a process of shifting has taken place of the coverts and remiges at the distal end of the forearm. This has resulted in carrying remiges 1-4 and the first and each succeeding horizontal row of coverts from 1-5 backwards and slightly downwards and outwards. Thus the original relations between the 5th major covert and its remex have been disturbed, the covert having shifted away from its remex, which has now become associated with the 6th covert. Thus the 5th, together with its ventral covert, appears to have lost its remex.

(3) The cause of this shifting is still a matter for investigation; it is possibly due to a slight secondary lengthening of the forearm.

Evidence in support of the above Conclusions.

We will now proceed to review the evidence in support of the hypothesis just submitted.

What follows has reference only to the developing remiges,
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and their coverts, of the forearm; those of the hand need not be taken into consideration in this connection.

In the eutaxic wing of the Common Fowl the earliest traces of feathers are those representing the remiges and their dorsal major coverts (Pl. 14. fig. 4). These form a double row along the post-axial border of the wing, the major coverts lying opposite the interspaces of the remiges, the ventral row of major coverts and the dorsal median and minor coverts appearing somewhat later, and the marginal last of all (Pl. 14. fig. 4). The arrangement of the median and minor follows that of the major coverts and remiges, so as to form a series of alternating rows, the feather rudiments of one row lying opposite the interspaces of the row in front of, and behind it. By the time the full complement of rows has been attained, however, this primitive arrangement in horizontal rows is somewhat masked, and the feather-papillæ appear rather to run in oblique rows sloping either from without inwards or *vice versa*, according to the view of the observer; but, as will be seen later on, when examining wings of other forms the obliquely-inward slope becomes finally adopted.

The wing of the Lapwing (*Vanellus cristatus*) (Pl. 14. fig. 1) agrees with that of the first stage (described above) of the Common Fowl in having only two rows of feather rudiments along the forearm, and, like this, it is also eutaxic. That is to say, no shifting has as yet taken place. The fifth major covert is not yet divorced from its remex. In a much later stage (Pl. 14. fig. 2) this severance has taken place: the wing is now diastaxic. Unfortunately, I have no intermediate stages between this and fig. 1. It is of interest to note, that the downward shifting in this case must have been but slight, as the intercalary is the 2nd and not the 3rd row of coverts, as was the case in the typical wing described on p. 239. Moreover, the feather rudiments seem to have travelled forward, inasmuch as the 1st cubital remex now lies on a level with a line drawn through the proximal end of the manus in front of the carpus; whilst in the younger stage the 1st remex lies proximad of this imaginary section.

The wing of the embryo Guillemot (*Lomvia troile*) (Pl. 15. fig. 2) is one of the most valuable of the whole series now in my possession; earlier stages than this are much to be desired. Here the remiges and major, median, and two (with faint traces of


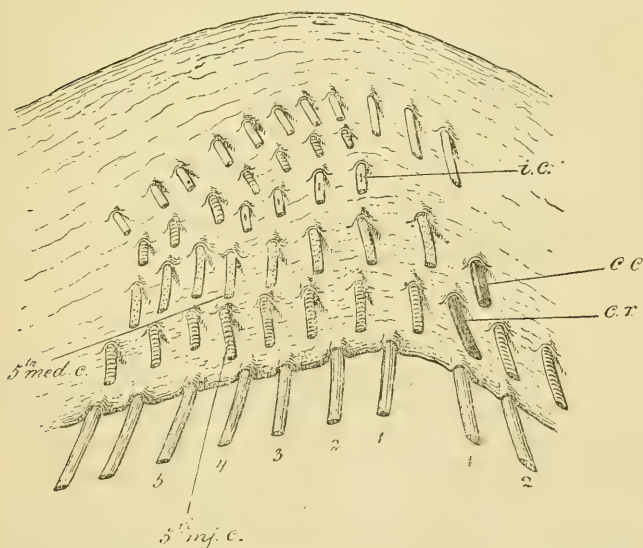
more) rows of minor coverts are all represented, but, as yet, the wing is undoubtedly eutaxic, though soon after this stage it becomes diastataxic. A foreshadowing of this is plainly visible at the stage under discussion. A reference to Plate 15. fig. 2 shows that the remiges 1-4 have already begun to move backwards through a small arc of a circle, the movement having been greatest at the distal end of the row, whilst the proximal end, represented by the 4th remex, has as yet scarcely moved at all. It may be expressed thus , the black line representing the original and the dotted line the new position. The disturbance is much more obvious in the row of papillæ immediately above the remiges—the rudimentary major coverts 1-5. These have become distinctly separated from the rest of the row proximad of this point. The disturbance of the rows preaxial to this of the major coverts is barely perceptible. There is yet no intercalary row. I have no stage between this and that of the nestling (woodcut, fig. 2).

Fig. 2.



Right wing, dorsal aspect, of nestling *Lomvia troile*, to show the diastataxic arrangement of the coverts.

The wings of the Pigeon (*Columba domestica*), Duck (*Anas boscas*), and Owl (*Syrnium aluco*) are selected as examples of typical embryonic diastataxic wings. In earlier stages of

these we must seek for confirmation of the course of development outlined in the case of the Plover and Guillemot.

In the Pigeon's wing (Pl. 15. fig. 1) the feather rudiments have arranged themselves in strongly marked transversely-oblique rows sloping inwards and presenting a strongly curved front towards the distal end of the wing. As yet, there are but faint traces of the marginal coverts. It is noteworthy that the transverse rows of coverts from 1-5 are more widely separated one from the other than is the case with the more proximal rows. The downward shifting of the anterior remiges and their coverts (1-5) is very marked. The intercalary row is the 3rd. This last is well seen in the wing of the nestling (Pl. 16. fig. 1).

In the wing of the Duck (*Anas boschas* var. *domestica*), Pl. 15. fig. 3, the intercalary is formed by the 3rd row of coverts, *i. e.* 1-5 of the minor coverts. There are faint traces of several more rows in addition to those in the figure. Compared with the adult wing, one very striking fact becomes apparent. It will be noticed that in the embryo wing (Pl. 15. fig. 3) the 1st median covert—that lying immediately above the first cubital remex and its major covert—lies over the base of metacarpal II., whilst the 2nd median covert lies just below the angle between the carpus and the distal end of the ulna. In the adult this spot comes to be occupied by the 1st median covert, that is to say, it apparently supplants the 2nd and takes its place. From this it would seem that we have indeed evidence of an increased lengthening of the forearm which can be measured by the distance from the 2nd to the 1st median covert.

A possible Objection.

Diastataxy, as we have endeavoured to show, is due, not as was supposed, to the loss of the 5th cubital remex, but to the shifting of the remiges and coverts lying to the outer side of this. The ultimate fate, however, of the remex in question has so far only been hinted at. *Exactly* what takes place during this shifting is difficult to make out, and will only be possible after a larger series of embryos have been examined. This much, however, seems certain,—that all the covert-feathers of the wing from the 6th inwards have moved outwards, one place, in the form of a series of obliquely transverse rows. Thus the transverse row which originally belonged to the 6th remex now

becomes associated with the 5th, that of the 7th remex with the 6th, and so on. A reference to the diagrams will make this clear.

At first sight, this outward movement seems to make rather a large demand upon the imagination, and to this extent to throw doubt on the interpretation of the facts recorded in this paper. The difficulty, however, is more imaginary than real. It simply means that the remiges in question become associated with transverse rows immediately in front instead of with those next behind. This must certainly happen in the case of the Guillemot’s wing. In the Duck and Pigeon’s wings (Pl. 15. figs. 1 & 3) this forward movement has already taken place. The ventral major coverts from the 6th inwards are subjected to the same forward movement as those of the dorsal surface. Thus the 5th remex lies between the 6th pair of major coverts, 6th remex between the 7th pair, and so on. The position of the ventral coverts 1–5 in these figures will illustrate the downward—ventralward—shifting of the feathers in this region.

The Carpal Covert and Remex.

A fixed point of no small value in the present connection is that afforded by the two feathers known as the carpal covert and the carpal remex (Pl. 14. fig. 2, *c.c.*, *c.r.*); inasmuch as, since they occur in wings of both types, they serve as valuable landmarks, and show, moreover, that the disturbance is to be sought for proximad of this point, and thus help to confirm the contentions of this paper. The significance of these feathers has been discussed by Wray (8), the present writer (5), and by Degen (1), who bestowed on them the names Carpal covert and remex, from their position on the carpus. Although feeling by no means certain on this point, I think the probability is that the “remex” is really correctly so named, and that it represents a feather more or less completely dwarfed and in course of disappearance. Its office—as a remex—has not entirely ceased. It is probably being slowly crushed out of existence by reason of its position, which is in the angle of the wing caused by the folding of the hand on the forearm. The 1st cubital remex of the Gallinæ is, like its carpal remex, and for the same reason, undergoing a similar process of reduction.

Explanations of Diastataxy.

The first recorded reference to diastataxy is that of Gerbe (3), who describes it in the following words :—" Chez les Rapaces, les Pigeons, les Échassiers, les Palmipèdes, il y a atrophie complète de l'une des remiges secondaires, et cette atrophie, qui paraît être originelle, porte invariablement sur la cinquième. Ses satellites, c'est-à-dire, sa couverture supérieure et sa couverture inférieure, prennent un développement normal et occupent leur place respective, comme si elles accompagnaient la plume qui fait défaut.

"Ni les vrais Passereux, ni les Zygodactyles (les Perroquets exceptés) ne présentent cette singulière anomalie."

My friend and late colleague, Mr. E. S. Goodrich, the Aldrichian Demonstrator of Comparative Anatomy at Oxford, took part with me for some time, in this investigation, and also formulated a theory of his own to account for the conditions which have been described and figured in this paper, and in justice to him, as well as because of its intrinsic value, I propose to endeavour to describe his theory here.

Briefly, he holds that the phenomena of diastataxy are due to a bifurcation of a row of feather-papillæ, probably the second—major coverts—starting at what is now the 5th major covert. Thus a double row was formed representing the present major and median coverts 1-5. This theory does not demand either shifting of remiges or coverts. Supposing the shifting of the former be proved, the presence of this "intercalary row," as he termed what are now major coverts 1-5, is still more easily understood. They have appeared to fill up the space between the row immediately in front and the remiges behind. Bifurcation of this kind occurs in the scale-covered forearm of Reptiles for instance : or, again, in the form of additional rows of ossicles in the manus of Ichthyosaurs.

Yet another attempt to solve this mystery is that of Degen (1). Though none will grudge this writer the credit of having evolved a very ingenious hypothesis, few probably will be found willing to adopt it. Degen carries us back to an imaginary quadri-dactyle manus in which each digit supported a set of remiges and major coverts. In course of time the 4th digit became suppressed and its remiges, 3 in number, migrated

inwards on to the ulna—ousting the cubital remiges 1–3. Next, the remiges of Digit II. moved inward on the ulna. Originally there were five of these, but the 5th, lying in the carpal angle between the bases of Metacarpals III. and IV., became suppressed,—just as occasionally happens in the case of the "carpal remex." The coverts of this suppressed 5th remex were retained. Feathers 1–4 only remained to migrate on to the ulna. The 5th is now only indicated by its coverts,—hence the diastataxic wing. The carpal covert and remex of existing birds represents the short 1st remex and covert of Digit III., which has travelled inwards along Mc. III. to rest finally on the carpal joint at the base of Mc. II.

Exceptions.

The wings of all birds are either eu- or diasta-taxic. Moreover, there is no known exception to the rule that, though a genus may include both forms of wings, it will be found that the species constituting that genus will group themselves, invariably, into two sections—those with eu- and those with diasta-taxic wings; for, as yet, individual variation in this particular is unknown. Therefore, the wing of any given species being found to be diastataxic, it may be certainly predicted that every individual of that species will also be diastataxic, and *vice versa*.

Amongst the Carinatae there are certain large groups every individual member of which, so far as is known, has diastataxic wings. These are :—

Pygopodes	= Divers, Grebes.
Tubinares	= Petrels, Albatrosses.
Herodiones	= Herons, Storks.
Steganopodes	= Cormorants, Gannets, Frigate-birds.
Phenicopteres	= Flamingoes.
Anseres	= Swans, Ducks, Geese, Screamers.
Accipitres	= Eagles, Hawks, Vultures, and Secretary-bird.
Ralli	= Rails.
Limicolæ	= Curlews, Plovers, Sandpipers, Auks, Gulls.
Pterocletes	= Sand-Grouse.
Megapodes	= Mound-builders.

To these may be added :—

Psittaci	= Parrots.
Striges	= Owls.
Caprimulgi	= Nightjars and Oil-bird.

Similarly the following are eutaxic :—

Tinami	= Tinamus.
Galli	= <i>Crow</i> , <i>Phasianus</i> , <i>Gallus</i> .
Turnices	= Hemipodes.
Opisthocomus	= Hoatzin.
Coccyges	= Cuckoos, Plantain-eaters.
Coraciæ	= Rollers, Bee-eaters, Motmots.
Bucerotes	= Hornbills and Hoopoes.
Trogones	= Trogons.
Colii	= Colies, or Mouse-birds.
Pici	= Woodpeckers.
Passeres	= <i>Eurylæmus</i> , <i>Pitta</i> , <i>Tyrannus</i> , <i>Menura</i> , <i>Atrichia</i> , <i>Corvus</i> .

The remainder of the Carinatae contain more or fewer exceptions—both eu- and diasta-taxic forms :—

Grues	= Cranes, Trumpeter, Seriema.
Columbæ	= Pigeons.

The Grues may be considered as a diastataxic group, the exceptions being :—

<i>Dicholophus</i>	= Seriema.
<i>Psophia</i>	= Trumpeter.
<i>Rhinochætus</i>	= Kagu.
<i>Eurypyga</i>	= Sun-bittern.
<i>Heliornis</i>	= Fin-foot.

These are all very aberrant types, whose systematic position is still a matter for investigation.

The Columbæ, like the Grues, are a diastataxic group, the only recorded exception being the genus *Columbula*.

The Coraciiform Alcedines (Kingfishers) and Macrochires (Swifts and Humming-birds) each contain genera the species comprising which include forms with both eu- and diasta-taxic wings. Thus amongst the Alcedines, in the genus *Ceryle*,

C. torquata, *C. rudis*, *C. alcyon*, and *C. maxima* are diastataxic; the remaining species of the genus are eutaxic. In the genus *Halcyon*, *H. vagans*, *H. chloris*, and *H. sancta* are diastataxic. *D. gigas* appears to be the only diastataxic member of the genus *Dacelo*.

The Macrochires comprise the Swifts (Cypseli) and the Humming-birds (Trochili).

The Trochili are all eutaxic.

The Cypseli are mostly eutaxic, but contain at least two genera possessing both forms:—

Dendrochelidon mystacea is diastataxic.

Acanthyllis collaris „

No satisfactory explanation of these exceptions has yet been offered, though some sort of an attempt was made by the late Henry Seebohm (6). He suggested that some diastataxic species may have become eutaxic by elimination of the coverts belonging to the missing fifth remex, thus removing all traces of their former condition. From the facts already educed in the preceding pages of the present paper, this particular interpretation must now be regarded as probably discounted. Before anything like a final explanation can be hoped for, we must wait till more material is at hand. A large series of embryo and adult species of those genera containing both forms of wings will probably settle the question. For the present, perhaps, the few suggestions advanced on p. 252 may be acceptable.

Facts correlated with Diastataxy.

According to Seebohm (6):—

1. No eutaxic bird has a webbed foot.
2. Birds which have abnormal plantar tendons contain both eu- and diasta-taxic species*.
3. There are very few diastataxic birds without an ambiens; but there are *no* eutaxic families that contain birds both with and without it†.

* Concerning 2 it may be remarked that this is equally true of birds having *normal* plantar tendons—Seebohm's term for plantar tendons in which the flexor perforans supplies each of the front toes.

† This depends upon the individual taxonomer—as to whether he eliminate the discordant elements.

4. Pelargomorphæ have normal plantars and are diastataxic.
5. Ægithomorphæ have normal plantars but are eutaxic.
6. Coraciomorphæ contain both diasta- and eutaxic forms.
Of four diastataxic families two contain both eu- and diasta-taxic species.

According to Degen :—

“Aquantocubitalism and Quintocubitalism seem to reflect on the presence or the absence of the 11th metacarpodigital flight-feather.” (All 11-primaried birds are diastataxic according to this author.)

According to Goodchild :—

The diastataxic wing is characterized by a peculiar interruption or faulting of the coverts of the dorsal surface.

Degen's contention is disproved by the fact that, as shown by Gadow (2), the following, though diastataxic, have only 10 primaries :—*Scopus*, *Eurypyga*, *Rallus*, *Ocydromus*, *Himantornis*, Psittaci, some Cypselidæ, *Caprimulgus*, and *Megapodius*.

Again, many Cypselidæ, *Eurylemus javanicus*, *Acanthyllis caudacuta*, and *Ceryla americana* have 11 primaries, but are eutaxic.

Goodchild's observation refers only to the external phenomena of the relative length of the feathers composing the different rows in this region of the wing. This “faulting” is not always visible in diastataxic wings, as is well seen in many Parrots for instance.

Some Degenerate Wings.

In the present connection it will be sufficient to survey this subject briefly. In the most perfect form of wing it will be noticed (Pl. 14. fig. 5) that the manus is longer than the forearm, and that the angle which the primaries form with the skeleton changes more and more from within outwards; the innermost remex lying at a right angle to, and the outermost parallel with, the long axis of the wing. Thus it comes about that the wing-area of the hand is as great as, or greater than, that of the forearm. Correlated with the form of the wing is the nature of the flight. Thus, in the Swifts and Albatrosses the wing is ribbon-shaped—very narrow from the pre- to the post-axial border, and much produced outwards. In birds like the Heron, the wing is very

broad, and the flight, though strong and capable of being sustained for long periods, is not so rapid.

It will be found that, the less the wing is used, the greater is the departure from this type. The manus shortens conspicuously, and the wing takes on a rounded form, making it difficult to distinguish primaries from secondaries in the outstretched wing. This is well seen in the wing of *Opisthocomus* (Pl. 16. fig. 2). Again, compare the wings of the Kagu, *Psophia*, *Ocydromus*, or the Common Water-Rail, with that of the more perfect Cranes; or the wings of *Coua*, *Phœnicophæa*s, and *Crotophaga*, *Turacus*, and *Musophaga*, with that of the Common Cuckoo; of *Stringops* with that of other Parrots, and so on. In all, the wing-area of the hand is lessened, markedly so, and the relative length of the secondaries is increased, whilst the primaries and their coverts grow shorter from within outwards. On discussing this matter with my friend and colleague, Mr. Eugene Oates, he drew my attention to the fact that this shortening and widening of the wing obtains in two non-migratory Indian Ducks.

The wings of the Rhea, Ostrich, Cassowary, and Apteryx afford evidence of still greater retrogression, passing from a relatively large wing, such as that of *Rhea*, in which may be distinguished primaries, secondaries, and coverts*, to the vestiges, more and more complete, in the Apteryx, Cassowary, *Æpyornis*, Moa, and *Hesperornis*.

The wings, then, both of the Ratitæ and the Carinatae, show that the reduction of the skeleton is soon followed by a reduction in the size, and then in the number of the remiges, and that this latter takes place at the extreme distal end of the primary and proximal end of the secondary series, where they become shorter and shorter and finally disappear.

* The pterylosis of the wing of *Rhea* I hope to describe shortly. It differs markedly from that of all other wings in that the dorsal coverts and remiges of the forearm are clustered together in strongly-marked obliquely-transverse rows separated by deep furrows one from the other. Furthermore, there remains to be settled one or two points touching the nature and homology of the remiges, and the disposition of the feathers in the carpal region. The ventral surface of the wing is bare.

In connection with the cubital remiges, it is interesting to note that these, in the Common Fowl, are, in the nestling, functionally preceded by their major coverts. This appears to be the case also in the young Pigeon, as is well seen in Pl. 16. fig. 1.

The probable Origin of the Diastataxic Wing.

We may now turn our attention to a discussion on the probable origin of diastataxy.

The primitive wing, I take it, was eutaxic, and resembled that of the Common Fowl in that it was clothed by numerous rows of covert-feathers; that of the Picariæ and Passeres is a specialization of a more primitive type, the number of rows of coverts having been reduced. Although, in these, the forearm may have increased in length, the remiges have decreased in number and become more widely spaced, and have developed broader vanes. Thus an equally efficient wing has been obtained with less expenditure of material.

The diastataxic wing is a modification of the eutaxic, and is possibly due to an increase in the length of the wing accompanied by a corresponding increase in the number of the remiges. It would seem more natural to assume, therefore, that all diastataxic wings have been derived from a common source; and thus this feature may be regarded as a sure sign of affinity, more or less remote, enabling us to classify all birds into groups eu- and diastataxic.

The existence, however, of what we may term eutaxic genera amongst diastataxic families is certainly a serious difficulty in the way of this hypothesis. For instance, *Columbula* is the only known exception amongst the Pigeons, which are diastataxic, though other exceptional genera may turn up, and the numerous instances of diastataxy amongst the Kingfishers and Swifts. It might be pleaded that *Columbula* has re-acquired a eutaxial form, by reduction in the length of the wing, and a similar reduction in the number, accompanied by a readjustment of the feathers. Note the position, for instance, of the 5th and 8th remiges in the wings of *Columbula* and *Columba*. That this is problematical, however, is shown by the wing of *Ocydromus*, which, though very greatly reduced in size, still remains diastataxic, like the rest of the Rails. Again, it is probable that the Megapodes, which are diastataxic, are somewhat closely related to the Game-birds, which are eutaxic. Apart from internal anatomy, they present the following points in common:—The remiges, in the nestling, are well developed and functional before the pre-pennæ of the trunk are replaced by the definitive contour-feathers. The 1st cubital remex develops much later in life than the rest of the

series, and is always much shorter than these. The Megapodes as we have just remarked, are diasta-, and the Game-birds eu-taxic. If the two are closely related, we might claim justification in holding that the arrested development of the 1st cubital remex was derived from a common source, and that diastataxy has been acquired by the Megapodes since then. If this interpretation be correct, it follows that we may hold it to be admitted that diastataxy may have arisen independently in different groups of birds,—a somewhat unlikely conclusion. The position into which we have drifted, then, may be stated as follows :—

The Class Aves, very early in the process of its differentiation, developed the phenomena of diastataxy, which has been retained by very different groups now regarded as only remotely allied. The presence of eutaxic forms in an undoubtedly diastataxic group, as in the case of *Columbula*, must be regarded as the result of a secondary re-arrangement of the wing-feathers, or as a reversion to the more primitive type of wing from which it was derived. Such admittedly aberrant eutaxic forms as *Psophia*, *Cariama*, *Heliornis*, must be regarded as more remotely allied to the diastataxic forms with which they are now associated than is generally believed. Diastataxy is probably an indication of consanguinity.

There are certainly difficulties in the way of acceptance of this view, perhaps the most formidable being the case of the Swifts and Kingfishers, the majority of which are eutaxic ; some genera, moreover, containing both eu- and diasta-taxic forms. We have to face two alternatives :—

- (1) That the group, whichever it may be, really belongs to the diastataxic stock, but that the majority of the species, like *Columbula*, have reverted to eutaxy ; or,
- (2) That diastataxy must be explained, in that and all other groups, as the result of the action of similar mechanical forces, upon a common type, and which may occur independently in different groups, and even different species of the same genus.

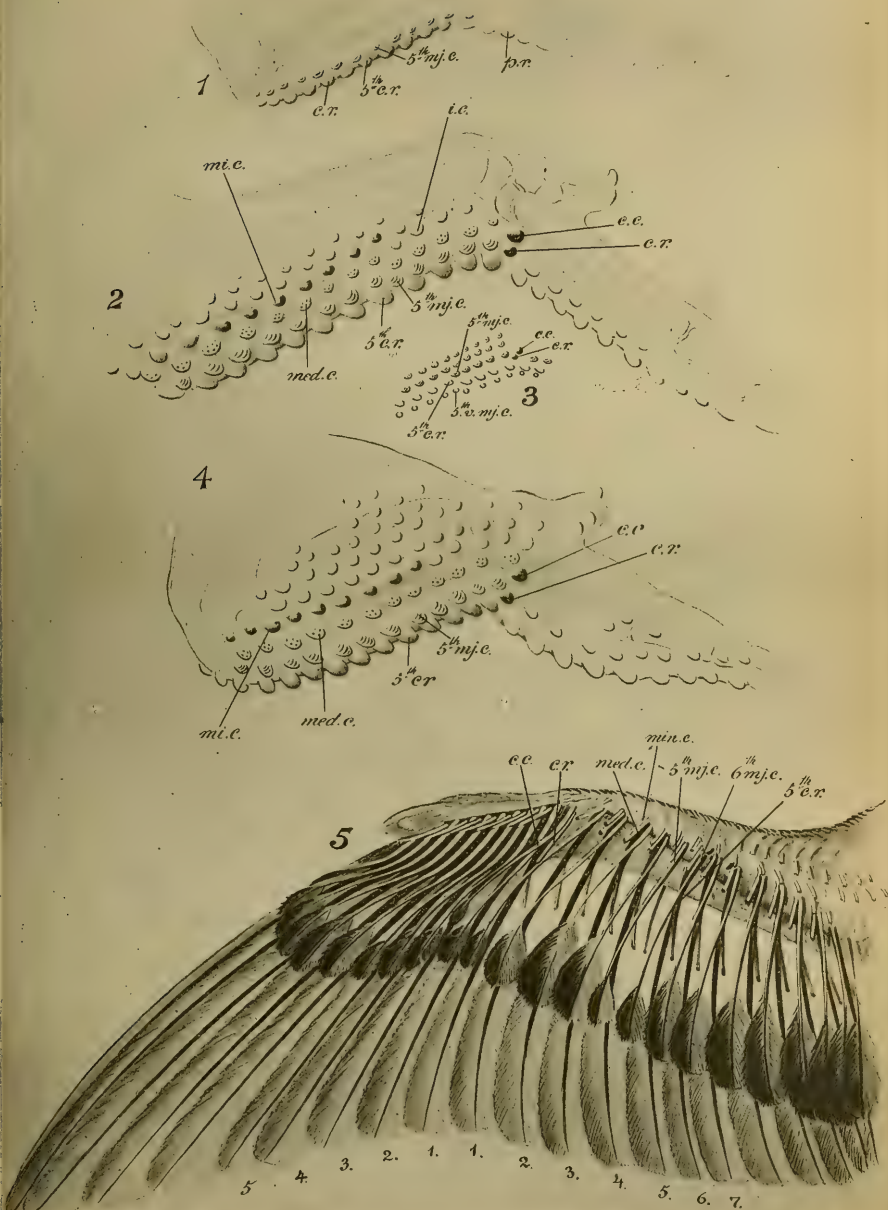
In spite of the objections which we may feel towards the first proposition, it seems more probable than the second, and more in harmony with the facts as a whole.

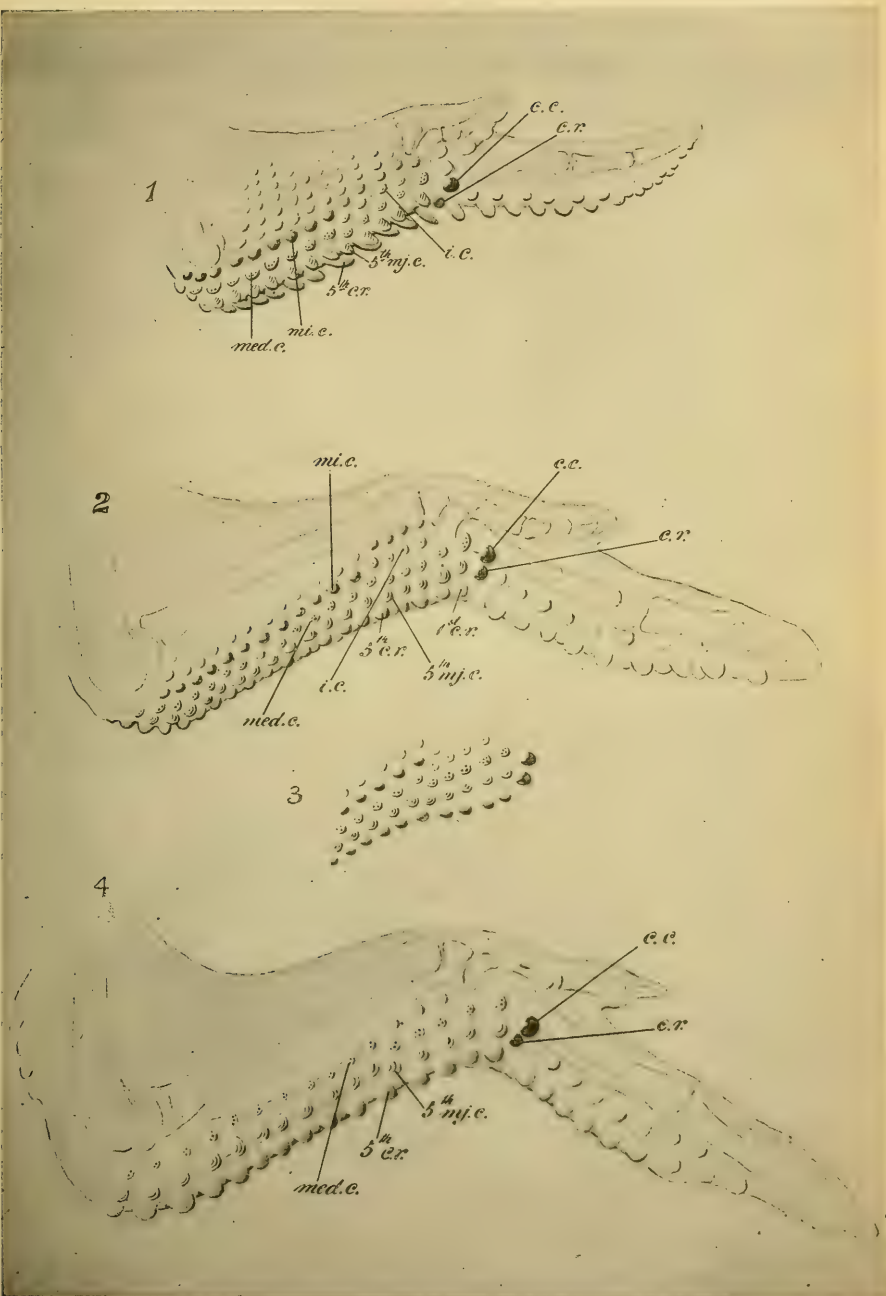
Diastataxy as a Factor in Classification.

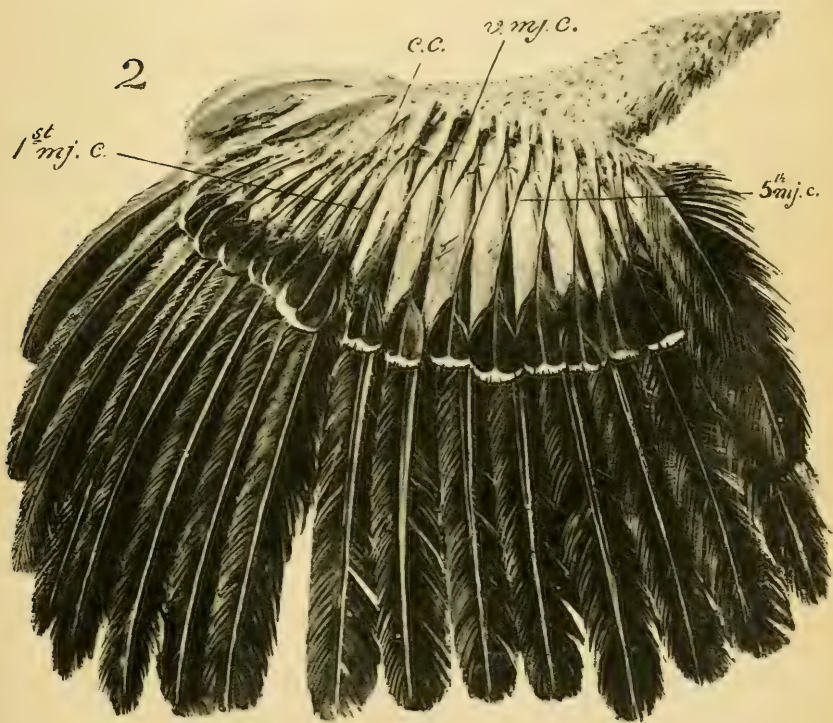
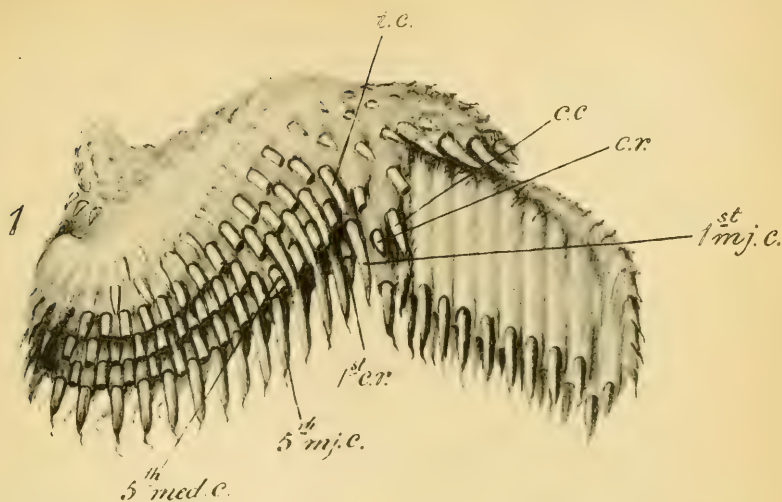
If it be true that diastataxy is an indication of a more or less remote degree of consanguinity, as has just been hinted, or, in other words, if diastataxic forms are more nearly related one to the other than those which are not, we may find this character, used with discretion, no small help in systematic work. I say used with discretion advisedly; for it is incontrovertible that the nature of the evidence from other sources makes it absolutely impossible to use this character as a primary factor, wherewith to divide the Class Aves into two great groups, eu- and diastataxic. But the presence of diastataxy in a little coterie of forms, admittedly related, but hitherto indiscriminately mixed with eutaxic, will be a sufficient reason to justify our separating them out to form a group by themselves, on the assumption that the character was inherited from a common source, and that they are therefore more closely related one to the other than to the neighbouring eutaxic forms. The presence of discordant elements in the shape of eutaxic forms amongst our now diastataxic groups—such as the Kingfishers, Swifts, and Pigeons—must be attributed to reversion or secondary readjustment of the feathers resulting once more in eutaxy. This is not as convincing as it should be; but it demands less of us than the alternative hypothesis, that diastataxy has been independently acquired wherever it occurs.

The result of the slight shifting here suggested is in no sense revolutionary in its tendencies. Amongst the Picarian forms it would bring together the Psittaci, the Striges, and the Caprimulgine forms associated therewith, the Swifts and Hummingbirds and the Kingfishers—all diastataxic, drawn from the ranks of eutaxic forms to constitute a little coterie by themselves. The Megapodes would be cut off from the remainder of the Galline forms, which are eutaxic, just as *Heliornis*, *Psophia*, *Cariama*, *Rhinochetus*, and *Eurypyga* remain as every modern systematist has left them—as isolated and aberrant groups in the neighbourhood of the Grues. *Cariama* remaining as a sort of sign-post pointing the way, as Beddard has recently shown, from the Grues to the Accipitres.

This scheme is doubtless open to criticism; but this may be said of every other.







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EXPLANATION OF THE PLATES.

Reference letters.

- c.c. = carpal covert.
 c.r. = carpal remex.
 i.c. = intercalary coverts, intercalary row.
 med.c. = median covert.
 mj.c. = major covert.
 v.mj.c. = ventral major covert.
 min.c. = minor covert.
 mi.c. = „ „

PLATE 14.

- Fig. 1. Right wing, dorsal aspect, of an embryo *Vanellus cristatus*, showing the first appearance of the feather-papillæ representing the remiges and major coverts of the forearm,—and indistinctly of the primaries.
- Fig. 2. The same in a more advanced stage of development. Several rows of coverts have now appeared, and "faulting" has already taken place. The wing is now diastataxic; in fig. 1 it is still eutaxic.
- Fig. 3. Portion of the right wing, dorso-ventral aspect, of an embryo *Machetes pugnax*, showing position of ventral major coverts.
- Fig. 4. Right wing, dorsal aspect, of an embryo *Gallus bankiva*, var. *domestica*. This is an eutaxic wing. The coverts have been marked as in the diastataxic forms for the purpose of comparison.

Fig. 5. Left wing, dorsal aspect, of an adult *Asio accipitrinus*, to show the typical, adult, diastataxic wing. Note the absence of a remex between the 5th pair of major coverts, and the marked gap between the 4th and 5th remiges.

PLATE 15.

Fig. 1. Right wing, dorsal aspect, of an embryo *Columba domestica*. This is markedly diastataxic. The shifting of the coverts is very distinct. Compare Pl. 16. fig. 1.

Fig. 2. Right wing, dorsal aspect, of an embryo *Lomvia troile*, at present eutaxic; but a study of the coverts shows that a shifting has commenced, the result of which ultimately reduces the wing to the typical diastataxic form. Compare this with the figure on p. 243, which shows the condition of the wing in the downy nestling.

The figure immediately below is drawn from fig. 2 to show the effect of a slight increase in the shifting of the coverts transforming the wing from the eutaxic to the diastataxic type, as seen in fig. 1.

Fig. 3. Right wing, dorsal aspect, of an embryo *Anas boschas*, var. *domestica*, decidedly diastataxic. No earlier stages were procurable.

PLATE 16.

Fig. 1. Right wing, dorsal aspect, of a nestling *Columba domestica*. Note the intercalary row of coverts, and compare with fig. 1, Pl. 14.; also the large size of the major coverts of the forearm as compared with the cubital remiges (1st c.r.), which have as yet only just begun to project beyond the surface of the wing.

Fig. 2. Right wing of adult *Opisthocomus*.

On the Discovery and Development of Rhabdite-"cells" in *Cephalodiscus dodecalophus*, McIntosh. By F. J. COLE, University College, Liverpool. (Communicated by Prof. G. B. HOWES, Sec. Linn. Soc.)

[Read 6th April, 1899.]

(PLATE 17.)

A SHORT while back Professor Herdman was kind enough to place in my hands some small pieces of *Cephalodiscus* for treatment and sectioning by modern microscopical methods. As interest in this unique form has been again aroused by the recent work of Masterman*, it was proposed to revise the whole anatomy of the polypide besides investigating the few points which a consideration of the literature showed to be unsettled.

* Q. J. M. S. vol. xl., 1897; Trans. R. S. Edin. vol. xxxix. pt iii., 1898.